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Engineer pioneer plants respond to and affect geomorphic constraints similarly along water-terrestrial interfaces worldwide

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ABSTRACT

Aim: Within river and coastal ecosystems worldwide, water, wind and sediment flows generate a shifting landscape mosaic composed of bare substrate, pioneer and mature vegetation successional stages. Pioneer-plant species that colonise these ecosystems at the land-water interface have developed specific traits to environmental constraints (response traits) and are able to modify habitat conditions by modulating geomorphic processes (effect traits). Changes in the geomorphic environment under the control of engineer plants often feed back to organism traits (feedback traits), and thereby ecosystem functioning, leading to eco-evolutionary dynamics. Here we explain the joint foundations of fluvial and coastal ecosystems according to feedbacks between plants and the geomorphic environment.

Location: Dynamic river and coastal ecosystems worldwide.

Method: Drawing from a pre-existing model of 'fluvial biogeomorphic succession', we propose a conceptual framework showing that fluvial and coastal 'biogeomorphic ecosystems' are functionally similar due to eco-evolutionary feedbacks between plants and geomorphology.

Results: The relationships between plant traits and their geomorphic environments within the different fluvial and coastal biogeomorphic ecosystems are identified and classified within a framework of biogeomorphic functional similarity according to three criteria: (i) pioneer plants develop specific responses to the geomorphic environment; (ii) engineer plants modulate the geomorphic environment; (iii) geomorphic changes under biotic control within biogeomorphic ecosystems feed back to organisms.

Main conclusions: The conceptual framework of functional similarity proposed here will improve our capacity to analyse, compare, manage and restore fluvial and coastal biogeomorphic ecosystems worldwide by using the same protocols based on the three criteria and the four phases of the biogeomorphic succession model.

61 INTRODUCTION

62 The geomorphic heterogeneity and variability of fluvial and coastal ecosystems (i.e.
 63 rivers, coastal and estuarine salt marshes and mangroves, coastal dunes) makes
 64 them among the most dynamic and productive ecosystems over extensive linear
 65 stretches of the Earth surface. These ecosystems at the interface between land and
 66 water (Fig. 1) encompass an enormous diversity of physical configurations, and
 67 species life forms and assemblages, reflecting the regional and local geological,
 68 geomorphic and bioclimatic settings. However, they also share common features
 69 reflecting the relation between plant dynamics and the geomorphic environment.

70 The structure and function of any physically disturbed fluvial or coastal ecosystem
 71 (e.g. meso to macrotidal conditions along the coast, piedmont to plain river reaches)
 72 result from feedbacks between plant dynamics and motion of water, wind, and
 73 sediment. Based on the strong feedbacks between plants and geomorphology, Balke
 74 *et al.* (2014) recently termed fluvial and coastal ecosystems ‘biogeomorphic
 75 ecosystems’ (BE), implying that ecosystem structure and function (i.e. habitat
 76 properties and species assemblages; matter and energy fluxes) are emergent
 77 properties of plant-geomorphic feedbacks. These feedbacks exist because of the
 78 ability of plants to adjust their characteristics to a geomorphologically-dynamic
 79 environment by genotypic or phenotypic adaptation, enhancing connectedness (i.e.
 80 degree to which the integrity of an ecosystem is controlled through internal feedbacks
 81 between small and large scale processes), and resistance and resilience (i.e. ability
 82 of the system to recover from physical disturbances) (see Holling, 1973). The BEs we
 83 define here relate exclusively to ‘geomorphologically dynamic ecosystems’, which are
 84 unstable and subject to frequent and regular physical disturbance. The BE concept is
 85 directly related to the ‘fluvial biogeomorphic succession’ (Corenblit *et al.*, 2007,
 86 2009a), which encompasses four phases of matter and energy organization in space
 87 and time (i.e. geomorphic, pioneer, biogeomorphic, ecological; Fig. 2). Each phase is
 88 linked to different time- and space-limited ecosystem structures and functions and is
 89 characterized by a specific set of interactions and feedbacks between plants and
 90 geomorphology.

91 The *geomorphic phase* is the rejuvenation phase following a flood, storm or tsunami,
 92 during which landform properties and stability are mainly defined by hydrodynamic
 93 and aerodynamic forces and intrinsic sediment cohesiveness. During this phase, the
 94 geomorphic environment controls plant diaspore dispersal (Fig. 2). During the
 95 *pioneer phase*, vegetation recruitment occurs on newly formed bare sediment
 96 surfaces, and the geomorphic environment controls seed germination and seedling
 97 survival and growth (Fig. 2). During the *biogeomorphic phase*, strong feedbacks

occur between plant and geomorphic dynamics as morphological and biomechanical characteristics of plants strongly interact with substrate cohesion and geomorphic flows of matter and energy. In the absence of major physical disturbances, changes in the geomorphic environment under the control of and resulting feedback on plants, result in the stabilization of the ecosystem during the *ecological phase* where biotic interactions dominate (Fig. 2).

It has been suggested that the ‘fluvial biogeomorphic succession’ model is relevant to dynamic rivers (Davies and Gibling, 2013; Gurnell, 2014; Bätz *et al.*, 2015), and also coastal (Kim, 2012; Balke *et al.*, 2014), and terrestrial BEs (e.g. lateral moraines, Eichel *et al.*, 2013), implying that it could be a useful common foundation for investigating many geomorphically dynamic ecosystems. However, this wide range of applicability does not imply that the quantity and intensity of interactions of plant - geomorphology feedbacks are the same in each BE because: (i) many different taxa and floristic assemblages are observed according to local and regional settings; (ii) at the same location, divergent trajectories in plant community assemblages can occur during the biogeomorphic succession, reflecting variations in initial biological and physical conditions; (iii) the duration and spatial extension of each phase of the biogeomorphic succession varies with the disturbance regime; (iv) different feedback loops exist between plants and geomorphology and related biogeomorphic stability according to the disturbance regime and plant characteristics.

Although BEs differ widely taxonomically around the world, comparable constraints can lead to convergent patterns of adaptive *traits* developing across taxa, as implied by the functional framework of adaptive CSR strategies proposed by Grime (2001). A ‘trait’ is any morphological, biomechanical, physiological or phenological feature, measurable at the individual level, from the cell to the whole-organism (Violle *et al.*, 2007). Many pioneer plant species have homologous traits optimizing their capacity for reproduction, survival and growth (i.e. fitness) within areas exposed to water, wind and sediment flows (Hesp, 1991; Bornette *et al.*, 2008). This does not mean that all co-occurring species have the same characteristics; alternative strategies may co-occur to cope with a stress, causing a few response trait-groups to co-inhabit a specific habitat (Stallins, 2005; Puijalon *et al.*, 2011).

We suggest that fluvial and coastal BEs are functionally similar as a result of dominant feedback mechanisms between the geomorphic environment and plant *response*, *effect* and *feedback* traits. Here, *response traits* are any plant attributes that provide an adaptive response to water or wind flow, sediment erosion, transportation and deposition, and lead to successful dispersal, recruitment, establishment and reproduction. *Effect traits* are morphological and biomechanical plant traits that induce a significant effect on the geomorphic environment. Within BEs, response and effect traits are strongly linked and may coincide because

successful colonization is a prerequisite for plants to affect the geomorphic environment and create biogeomorphic feedbacks. For example, a multi-stemmed flexible morphology may increase the capacity of a plant to resist hydrodynamic forces (response) while also affecting sediment fluxes and topography (effect). We define *feedback traits* as those that provide a response to the modification they induce in the geomorphic dimensions of their niche.

Based on a critical review of ecological and geomorphological investigations of fluvial and coastal ecosystems across the world, we highlight below how different engineer (*sensu* Jones, 2012) pioneer plants respond to wind, water and sediment flows and affect geomorphic processes in a similar way, leading to an enhanced understanding of the role of plant traits in geomorphologically-dynamic ecosystems that opens new research perspectives.

The trait-based approach we propose here to define a BE is founded on three key criteria related to the geomorphic setting and to the nature of its relation with plants (Fig. 3): (1) plants must have developed specific response traits to the geomorphic environment and its disturbances; (2) they must display effect traits that control the geomorphic environment; (3) they must display feedback traits to these biotic-controlled geomorphic changes. In the presence of a biogeomorphic ecosystem *sensu stricto*, all three criteria have to apply to the plants. In this paper the term 'trait' (response, effect and feedback) will be used as recommended by Violle *et al.* (2007) specifically at the level of individuals. However, responses, effects and feedbacks can relate to varying spatio-temporal levels including individuals (i.e. plastic and evolutionary adjustments of traits), populations (i.e. changes in survival-mortality ratio, age structure, cover) and communities (i.e. adjustments in short and long-term floristic assemblages and biodiversity).

CRITERION 1: RESPONSE TRAITS OF PIONEER PLANTS TO THE GEOMORPHIC ENVIRONMENT

BEs are unstable and subjected to a physical disturbance regime

Most fluvial and coastal BEs consist of unconsolidated sediment and are subjected to a natural disturbance regime (i.e. variations in river water flow, tidal currents and waves, or wind), incorporating both low to medium magnitude variations in hydrodynamic and aerodynamic forces, and also less predictable medium to high magnitude exceptional fluctuations during extreme events (Naiman *et al.*, 2008). Within rivers, the disturbance regime corresponds to seasonal variations in water level and velocity and medium intensity flow pulses, and isolated intense flood events. Within salt marshes and mangroves, it corresponds to daily and seasonal variations in tidal water level and isolated storm or tsunami events. Within coastal

dunes, it relates to seasonal variations in extratropical and tropical storm tracks, mean wind velocity and direction, and isolated storm and tsunami events (Balke *et al.*, 2014).

Plant assemblages and their corresponding functional structure within BEs vary along gradients of exposure to these physical disturbances (Fig. 4), and also along gradients of stress related to anoxia, salinity, drought or competition. Within fluvial ecosystems these gradients are superimposed onto transverse gradients of hydrogeomorphic connectivity and topography from the channel to the floodplain (Bornette *et al.*, 2008; Fig. 4a). Within salt marshes and mangroves they are superimposed onto gradients of wave energy, tide influence, micro-topography and salinity from the seashore to inland (Thom, 1967; Fig. 4b, c). Within coastal dunes they are superimposed onto gradients of exposure to aerodynamic and hydrodynamic forces, topography and salinity from the shoreline to inland (Stallins & Parker, 2003; Hesp & Martínez, 2008; Kim & Yu, 2009; Fig. 4d).

The disturbance regime acts as an environmental filter of response traits

Engineer plant response traits adapt over the long term to the most regular component of the physical disturbance regime (Lytle & Poff, 2004; Naiman *et al.*, 2008). At the establishment stage, selection among the pool of species reflects response traits that favour high net productivity, dispersal, reproduction and survival rates. Many pioneer riparian and coastal species share equivalent response traits (e.g. sexual/vegetative reproduction; body and seed size) related to their morphology, physiology and phenology (Table 1). Plant trait optimization to water, wind and sediment flows does not necessarily result in convergence, but may also cause divergence of traits based on the disturbance regime, resulting in contrasts in the way pioneer plants and flows interact and modulate geomorphic processes and landforms (Bouma *et al.*, 2005, 2013; Stallins, 2005). At the earlier stages of the biogeomorphic succession, and in comparison to biological disturbances such as grazing and bioturbation by animals, the disturbance regime represents the pre-eminent selection pressure for riparian and coastal plants (1 in Fig. 3). It acts as a strong environmental filter of response traits throughout the biogeomorphic succession (Fig. 2; Table 1).

Pioneer plants can respond to physical disturbances and sustain viable populations through resistance and resilience mechanisms (Table 1), where resistance is the capacity of the plant to maintain its structure or biomass during disturbances, and resilience is the capacity of the plant to restore its structure or biomass after disturbances. In many cases high frequency disturbances of low to medium intensity are essential for the expression of response traits favouring plant resistance and resilience within fluvial and coastal BEs.

Plant response traits during the geomorphic phase

During the geomorphic phase, the geomorphic environment controls the biotic compartment (Fig. 2), especially diaspore dispersal, which is a crucial process that may coincide with predictable (seasonal) hydrogeomorphic or aerodynamic conditions that guarantee successful recruitment. Recruitment of pioneer populations in BEs requires the coincidence of diaspore release with adequate abiotic conditions. Phenological response traits of many plant species are intimately coupled to the periodicity and intensity of hydrogeomorphic constraints (Bornette *et al.*, 2008; Maun, 2009; Balke, 2013; Table 1). In order to cope with the inherently stochastic nature of the geomorphic phase, pioneer engineer plants generally employ opportunistic strategies (*sensu* Grime, 2001; Table 1). Diaspores are mostly produced in very large numbers and can remain viable for a long period. Their production and release are usually well synchronized with the disturbance regime and climate patterns. For example, within temperate river environments seed production and release by riparian *Populus* and *Salix* spp. coincides with the period following predictable annual floods (Lytle & Poff, 2004; Stella *et al.*, 2006) so that their small, buoyant seeds are transported by water and wind to newly-formed bare sediment surfaces. In coastal environments, diaspores (seeds, rhizomes, stolons, roots and branches) are mainly hydrochorous (Table 1). They are mobilized and transported by water, usually during floods and storms (Maun, 2009), and they maintain their capacity to germinate and sprout after transportation in salty water (Guja *et al.*, 2010). Within mangroves formed by *Rhizophora* and *Avicennia* spp., massive propagule production occurs during the wet season when salinity is low (Fernandes, 1999). Within coastal dune BEs, certain annual species release large quantities of seeds during the period with the highest availability of bare moist coastal substrates that are required for seed germination (Wagner, 1964).

Plant response traits during the pioneer phase

The transition toward more vegetated states that accompanies amelioration of the harsh abiotic environment is highly variable because initial habitat conditions strongly affect initial plant establishment, and the transition requires adequate physical conditions related to combinations of morphological, biomechanical and physiological response traits (Table 1), and also proximity to a diaspore source or dispersal pathway. In rivers (Cooper *et al.*, 2003), salt marshes and mangroves (Balke *et al.*, 2014), dynamic interactions between numerous fluctuating climatic and geomorphologic parameters lead to multiple possible pathways of seedling recruitment on bare surfaces that are only colonised in sufficient numbers every few years. Recruitment success can change with quite small variations in hydrogeomorphic parameters. Similarly, in dune settings, seedling recruitment depends upon the contrasts in wave energy under winter and summer wave regimes

and the net balance between seasonal patterns of sediment erosion and deposition with subsidies from seaweed and other organic wrack debris enhancing the likelihood of seedling recruitment (Davidson-Arnott & Law, 1990).

Once seeds and propagules (e.g. rhizomes, stolons, roots) of pioneer engineer species reach a freshly exposed, bare surface they germinate or anchor almost immediately, whether on alluvial bars within fluvial BEs (Gom & Rood, 1999), on mud flats within mangroves (Guja *et al.*, 2010) or on the upper beach within coastal dune BEs (Maun, 2009). Many riparian (e.g. *Populus* and *Salix* spp.), salt marsh (e.g. *Spartina* and *Puccinellia* spp.) and mangrove tree (*Sonneratia* and *Avicennia* spp.) species are highly clonal. The ability to easily resprout is a major advantage for colonizing areas heavily disturbed by extreme disturbance events.

During the early stage of the biogeomorphic succession, emerging seedlings or sprouts remain highly exposed to fluctuating hydrodynamic and aerodynamic forces, sediment dynamics and substrate moisture (Mahoney & Rood, 1998; Bouma *et al.*, 2009; Balke *et al.*, 2014). Following germination, rooting anchorage may develop very quickly ensuring a strong, early mechanical and physiological resistance to hydrodynamic or aerodynamic forces, sediment burial or to stress induced by ground and soil water fluctuation (Westelaken & Maun, 1985; Guilloy *et al.*, 2011). For example, many vivipar propagules of mangrove trees have pre-formed roots that ensure almost immediate anchoring and morphological plasticity is already important. Balke *et al.* (2013) showed that sediment burial increases shoot growth and erosion increases root growth of mangrove tree seedlings, increasing their survival chances according to the disturbance regime. Seedling growth rate is also crucial. Balke *et al.* (2014) identified two conditions for successful recruitment within fluvial and coastal BEs: (i) the coincidence of dispersal events with sufficient hydrodynamic or aerodynamic force to bring an adequate number of diaspores to suitable sites; (ii) a sufficiently long period for seedlings to germinate and establish that is free of destructive disturbances. This window of opportunity can be a few days to a few months in fluvial BEs and a few hours to a few days within salt marshes, mangroves and coastal dunes (Balke *et al.*, 2014). Therefore, colonization events can potentially be predicted when plant response trait information on germination, root growth and plant stability are linked to environmental variables such as water level, wind speed and salinity.

Plant response traits during the biogeomorphic phase

Plants that are adapted to unstable and fluctuating geomorphic environments have high phenotypic variability and plasticity, including modulation of above and belowground biomass allocation, architecture, and the biomechanical and physiological properties of organs, which ensure their resistance to water flow and

wind, sediment erosion, burial and sand abrasion (Bornette *et al.*, 2008; Maun, 2009; Table 1). Trait changes result from trade-offs between the need to resist abrasive and tractive mechanical forces, prolonged submersion, and sediment erosion and burial; to acquire resources; and to adapt their reproductive strategy (clonal vs. sexual) to disperse and establish efficiently.

Response traits that support resistance to mechanical constraints are mainly morphological and biomechanical, including strengthening tissues; stiff stems; prop, stilt and kneed roots; small and streamlined leaves and canopies; brittle stems with breaking points (Bouma *et al.*, 2005; Bornette *et al.*, 2008; Maun, 2009; Table 1). Pioneer plants are highly resilient to damage. For example, they can resprout from damaged stumps and rhizomes (Nzunda *et al.*, 2007; Moggridge & Gurnell, 2009), or they can show a plastic morphological and biomechanical response (i.e. thigmomorphogenesis) to repetitive mechanical forces from water or wind, increasing their resistance to breakage and uprooting. Response trait variations can express a trade-off between tolerance (e.g. large stem cross-section, production of strengthening tissues, increase in root biomass) and avoidance (e.g. increase in stem flexibility, aerial biomass reduction, morphological reconfiguration within the fluid) (Puijalon *et al.*, 2011), and can have major consequences for a plant's ability to fit to disturbance (Bouma *et al.*, 2005; Stallins, 2005; Gurnell, 2014). In the case of absence of major disturbances, the biogeomorphic phase can be followed by the ecological phase where biotic interactions (e.g. competition) are dominant and physical disturbances rare.

CRITERION 2: EFFECT TRAITS OF ENGINEER PLANTS THAT MODULATE THE GEOMORPHIC ENVIRONMENT

Within BEs, the control of ecosystem structure and function by engineer plants is achieved through durable modification of the habitat (2 in Fig. 3). Three main categories of effects of engineer plants on their geomorphic environment can be identified and are explored further below: (i) increase in sediment retention and cohesiveness; (ii) fluid stress divergence; and (iii) physicochemical modification and biogenic accumulation.

Increase in sediment retention and cohesion

In fluvial and coastal BEs, the roots and rhizomes of plants increase sediment cohesiveness (Polvi *et al.*, 2014), offering protection against erosion, particularly where pioneer plants have dense root systems and flexible, flattening or creeping canopies. A very-well developed literature demonstrates how such engineer plants obstruct water and wind flows, reducing shear stresses at the ground surface and trapping matter 'within-site' (within their canopy) and 'off-site' (downstream or

downwind of the vegetation stand). Within-site effects on sediment trapping and the extent of downstream or downwind deposition vary with canopy structure, fluid properties, and sediment transport (Bouma *et al.*, 2013; Nardin & Edmonds, 2014). Individual woody plants or isolated herbaceous patches locally impact sediment transport forming small hummocks or coppice dunes. Isolated groups of dense ligneous and herbaceous perennials form pioneer islands and discontinuous benches at river channel margins (Gurnell *et al.*, 2012); large hummocks within salt marshes (Bouma *et al.*, 2009); islands and platforms within mangroves (Fromard *et al.*, 2003); and large coppice dunes, incipient foredunes or parabolic dunes within coastal dune systems (Baas, 2007; Hesp & Martínez, 2008). At larger spatial and temporal scales, between catastrophic floods, storms and tsunamis, engineer plants interact with sediment transport to create large stabilized vegetated islands and floodplains in fluvial BEs, and plain dunes and inter-tidal stabilized flats in coastal BEs. Pioneer biogeomorphic units also induce off-site effects by protecting downstream and downwind areas and allowing further recruitment. This is illustrated, for example, by the way in which pioneer islands colonized by *Populus nigra* and *Salix* spp. within the high-energy Tagliamento river (Northern Italy) enhance seedling and sapling survival in sheltered areas (Moggridge & Gurnell, 2009).

Topographic changes induced by engineer plants can reflect species-specific morphology, biomechanics and growth patterns, as illustrated by experiments with tamarisk (*Tamarix* spp.) and cottonwood (*Populus fremontii*) disposed within a mobile sand-bed flume (Manners *et al.*, 2015), where the shrubby morphology of tamarisk resulted in greater reductions in near-bed velocities and sediment flux rates. In another flume experiment the spatial pattern of salt marsh sediment erosion and deposition was observed to vary with morphological and biomechanical effect traits and growth patterns of *Spartina anglica*, *Puccinellia maritima* and *Salicornia procumbens* (Bouma *et al.*, 2013). Furthermore, Perry & Berkeley (2009) showed that the planting of *Rhizophora mucronata* in SW Indian Ocean mangroves led to structural changes, particularly an increase in fine sediment and organic-matter in the intertidal substrate. Krauss *et al.* (2003) found that fine sediment accretion rates varied with root morphology in Micronesian mangrove forests, particularly with the prop roots of *Rhizophora* spp., root knees of *Bruguiera gymnorhiza*, and pneumatophores of *Sonneratia alba*. Lastly, in coastal dunes of the USA Pacific Northwest, Zarnetske *et al.* (2012) observed that dune shape varies with the ability of certain species (*Elymus mollis*, *Ammophila arenaria* and *A. breviligulata*) to trap sand and their growth habit in response to sand deposition (see also Maun, 2009; Pelletier *et al.*, 2009).

Fluid stress divergence

Resistant engineer plants also induce turbulent scouring in their surroundings. Such stress divergence plays a major role in increasing landscape complexity and diversity and forming newly-exposed bare substrate locally during the biogeomorphic phase. Pioneer trees that establish on river gravel bars induce sediment scours upstream and laterally (Gurnell *et al.*, 2005). Within coastal BEs colonized by vegetation, entrenched channels are formed through erosion between laterally expanding and aggregating tussocks and vegetated levees (Temmerman *et al.*, 2007). D'Alpaos *et al.* (2007) noted that vegetation controls tidal drainage network formation and geometry according to the combined effects of within-site sediment binding and off-site flow diversion and concentration by plants. Furthermore, dune topography controlled in part by dune-building plants can also redirect future overwash and shape local patterns of erosion as well as accretion (Davidson-Arnott & Law, 1990).

The combination of local and downstream or downwind protective-accretive and off-site erosive effects of plants control spatial and temporal self-organization of BEs mainly during the biogeomorphic phase (Temmerman *et al.*, 2007; Bouma *et al.*, 2009, 2013; Kim, 2012; Corenblit *et al.*, 2015). It has been further suggested that the pattern of sediment trapping and erosion corresponds to a biogeomorphic scale-dependent feedback. Such feedbacks occur within ecosystems when the landform pattern is reinforced and maintained by a positive feedback in resource acquisition at the local scale (within-site) and when an inhibiting feedback occurs at a larger scale (off-site, at the margins). Evidence for the landscape consequences of scale-dependent feedbacks in BEs is especially strong for rivers (Gurnell, 2014) and salt marshes (Temmerman *et al.*, 2007; Bouma *et al.*, 2009, 2013), although biogeomorphic self-organization also occurs within sand-dune systems (Baas, 2007).

Physicochemical modification and biogenic accumulation

Plants induce physicochemical modification of the habitat and biogenic accumulation within BEs. Such engineer effects in different fluvial and coastal BEs enhance local biochemical activity improving ecosystem processes and ambient conditions within engineered sites.

For example, in high energy rivers, Bätz *et al.* (2015) showed how organic matter input within stabilized pioneer landforms enhance the transition from landforms dominated by fresh sediment deposits towards soil-covered biogeomorphic units such as floodplains. Within salt marshes and mangroves, where the tidal range and the minerogenic sediment input are limited, engineer plants alter the topography through peat-like substrate formation. Morris *et al.* (2002) suggested that coastal engineer plants can control their relative elevation through biomass modulation in

order to keep up with sea-level rise. Several studies have also shown that many salt marshes and mangroves are able to maintain their surface elevation within the inter-tidal zone over long periods of sea level rise through the modulation of root and aerial biomass production by plants, and associated peat formation and vertical land-building (Larsen & Harvey, 2010; Marani *et al.*, 2013). Furthermore, fixed dune systems are characterized by the existence of soil catenas that reflect feedbacks between sediment characteristics, topography, drainage conditions and vegetation (Maun, 2009).

CRITERION 3: FEEDBACK TRAITS ASSOCIATED WITH BIOTIC-CONTROLLED GEOMORPHIC CHANGES

Geomorphic changes that occur under biotic control during the biogeomorphic phase feed back into the ecosystem at varying levels (i.e. individual, population and community; 3 in Fig. 3). Changes in individual traits, population parameters and community properties are not just a passive response to initial habitat conditions. During succession, pioneer engineer plants, by controlling landform construction, affect gradients of strategies, population and community dynamics within BEs.

Individual and population plant response to sediment accretion they enhance

Many pioneer engineer plant species that establish within fluvial and coastal BEs require sediment burial to enhance their anchorage, to favour more vigorous growth, and to increase their chances of reaching sexual maturity (Maun, 2009; Corenblit *et al.*, 2014). One or more plant individuals that initiate formation of an embryo fluvial or coastal island, a small shadow dune, or a tussock, can exploit the freshly deposited sediment by developing adventitious roots and rhizomes to stabilize a viable population in a geomorphologically-unstable environment (Maun, 2009; Rood *et al.*, 2011), and lead at the micro- to meso-scales to a positive feedback of landform construction, vegetation growth (i.e. feedback traits) and population demographic stabilization. This is exemplified by *Populus* and *Salix* spp. within river environments (Corenblit *et al.*, 2014; Gurnell, 2014), subspecies of *Spartina patens* within salt marshes (Wolner *et al.*, 2013) and *Avicennia germinans* in mangroves (Fromard *et al.*, 2003). This is also well exemplified in coastal dunes by grass species. For example, Zarnetske *et al.* (2012) noted that aerial growth of pioneer engineer plants is favored by sediment deposition they enhance in coastal dunes of the Pacific Northwest of the USA. Vertical canopy growth was observed to be stimulated within a few weeks following burial, and the dune building capacity of engineer species was linked to a specific biogeomorphic feedback between plant growth and architecture, and sediment deposition.

Through spatially explicit feedbacks between vegetation and topography, the diversity of plant traits can canalize patterns of plant establishment and persistence in BEs and lead to different biogeomorphic domains of stability (Stallins, 2005; Corenblit *et al.*, 2009a; Wolner *et al.*, 2013; Vinent and Moore, 2015). For example, in coastal dunes where overwash forcing is more frequent, plants displaying horizontal growth in response to sediment burial (i.e. ‘burial tolerant stabilizers’) are reinforced because they enhance a flat topography with low resistance that promotes the likelihood of overwash. Where overwash disturbance is less frequent, plants with vertical growth are favoured by sediment burial (i.e. ‘landform builders’) since they promote positive-relief topographies. *Ammophila arenaria* produces dense vertical tillers when buried, which favor its development and the development of tall narrow foredunes, while the less dense lateral growth of *A. breviligulata* builds shorter but wider foredunes.

Plant community response to geomorphic changes

Sediment accretion and related topographic aggradation under the control of engineer plants also control plant assemblages at community level through the exclusion of species by burial, the decrease of exposure to disturbance and vegetation shading (Corenblit *et al.*, 2014, 2015). Within rivers and coastal BEs, it is the combination of sediment accretion, topographic rise and vegetation growth that leads to the main changes in the physicochemical properties of the habitat and in floristic assemblages during the biogeomorphic phase (Tabacchi *et al.*, 2000; Gurnell, 2014). For example, when foredunes develop within coastal dunes, they lower the amount of sand and salt spray transported inland, facilitating the incursion of woody vegetation in their lee-protection. At the same time, as control by physical constraints diminishes, biogeochemical controls become prominent, with organic matter accumulation and shifts in habitat diversity from a horizontal (within the habitat mosaic) to a vertical (soil to canopy) development (Bätz *et al.*, 2015).

Eco-evolutionary feedbacks

Engineer species certainly change selection pressures within the environment (Wright *et al.*, 2012). Key parameters of the physical environment within BEs are strongly controlled by the effect traits displayed by pioneer engineer plants. We suggest that the long-term history of adaptive changes related to ecological and evolutionary feedbacks between organism response, effect and feedback traits, and geomorphic dimensions lead to the emergence of BEs as self-organized adaptive ecosystems *sensu* Holling (1973).

Therefore, the geomorphic gradients and associated community assembly rules and functional structure that are observed within fluvial and coastal BEs, need to be considered as emergent properties of short-term (ecological) and long-term (eco-

evolutionary) top-down and bottom-up abiotic-biotic feedbacks (Corenblit *et al.*, 2015). Recent palaeontological studies (e.g. Davies & Gibling, 2013) have shown that the evolutionary trajectory of engineer plant traits and many other passenger taxa (microorganisms, fauna and flora) has been modulated over the long term within fluvial BEs by the niche-constructing activity of engineer plants and the resulting network of diffuse co-evolution among the different taxa (Corenblit *et al.*, 2014, 2015). Consequently, eco-evolutionary (*sensu* Erwin, 2008) concepts such as niche construction (Odling-Smee *et al.*, 2003) certainly represent a useful framework for analyzing feedbacks between organisms and geomorphology within fluvial and coastal BEs.

FUTURE RESEARCH TASKS

The proposed model of biogeomorphic functional similarity of plant response, effect and feedback traits has the potential to become an operational framework for the articulation of future research priorities of fresh- and saltwater-terrestrial interface systems. This global model of biogeomorphological ecosystem (BE) functioning is also conceived to contribute to the improvement of management and restoration strategies. In order to achieve these goals, we list below future tasks to be investigated for each of the three criteria that define BEs.

Criterion 1: defining the window of opportunity of engineer species

The habitat conditions leading to successful germination and growth of key engineer species must be quantified *in situ*. The quantification of the factors affecting recruitment of plants within fluvial and coastal environments has begun a long time ago. The 'recruitment box' model for fluvial systems of Mahoney & Rood (1998) and the homologous model of a 'window of opportunity' for all four biogeomorphic ecosystems proposed by Balke *et al.* (2014) emerged from previous studies. They are both useful operational conceptual frameworks for analyzing the relationship between environmental variability and vegetation recruitment during the pioneer phase of the biogeomorphic succession. The hierarchy of the same local and regional factors affecting plant dispersal, germination, initial growth and survival in different world locations must be established. Response traits that provide an advantage must be identified and quantified simultaneously *in situ* and *ex situ* in controlled conditions to isolate the key factors (e.g. Guillo *et al.*, 2011; Balke *et al.*, 2014). Quantitative comparison between different BEs will lead to a formal definition of the worldwide envelope of environmental conditions leading to successful recruitment of engineer plant species that can modulate their geomorphic environment. The frequency histogram of the number (and related functional status) of recruited engineer species along geomorphic niche dimensions, such as for

example mean duration and frequency of disturbances, will be a useful tool for identifying functional groups of response to geomorphic constraints.

It is also necessary to quantify thresholds of resistance of colonizing engineer plants to the mechanical and physiological constraints imposed by water and wind within BEs. This remains challenging because of dynamic interactions between the fluid, the sediment and the plant (Corenblit *et al.*, 2007) and because of the latter's high phenotypic variability and plasticity. Quantifying these thresholds will also require *ex situ* flume experiments using key engineer species.

Criterion 2: linking plant traits and landform properties

Establishing quantitative understanding of the relation between engineer plant response, effect and feedback traits, and landform geometry, dynamics and physicochemical properties is also a priority. Effects of engineer plants on geomorphology must be quantified by considering causal linkages with resulting feedback traits. We consider that the geometrical and physicochemical properties of each category of small to large scale coastal and fluvial landforms (e.g. pioneer fluvial or mangrove islands, hummocks, copies dunes and foredunes) are modulated across the world by the same basic processes but according to specific traits of the local pioneer engineer plant species. These landforms that develop under the control of engineer plants thus exhibit a large range of possible deviations in size, shape, texture, physicochemical characteristics, resistance and resilience relative to their theoretical physical state. Such deviations are likely to be biologically functional for the engineer species and potentially for passenger species. Therefore, it is an important goal to test the hypothesis of engineered landform functionality at the global scale (Corenblit *et al.*, 2015). This will be achieved by analyzing correlations between plant growth performance and type of reproduction, and the frequency histogram of landform properties such as relative elevation, exposure to disturbances (Bertoldi *et al.*, 2011) and physicochemical properties (Bätz *et al.*, 2015). Ultimately, the correspondence between genetic variability of engineer plant species and landform properties must be analyzed to establish a genetic basis of the variation of landform geometry and dynamics.

Another important research objective related to criterion 2 is to test the effects of plant trait diversity on the function of landform construction and ecosystem stabilization. Plant functional traits enhancing sediment cohesiveness and trapping often combine at the community level and form functional units with varying sediment stabilization and trapping capacities (Corenblit *et al.*, 2009b). Population thresholds of sediment stabilization and trapping might be overridden by the combination of different traits at the community scale. The combination of varying traits, and thus varying genomes, is likely to increase the stability of the biogeomorphic function of

sediment trapping and landform construction. The presence of different functional types and genomes may potentially also lead to the persistence of fluctuating biogeomorphic conditions over larger areas (Stallins, 2005). These relationships between trait diversity and functional stability of BEs require further investigation worldwide.

Criterion 3: testing the hypothesis of niche construction

Landform construction during the biogeomorphic succession and related variation in mean trait value and vegetation assemblage are viewed here as an emergent property of ecosystems originating from ecological (10^{-1} to 10^3 years) and evolutionary ($>10^4$ years) feedbacks between genes, organisms and the geomorphic environment (for more details see Corenblit *et al.*, 2014, 2015). We acknowledge that formal evidence of this statement is lacking but we stress that the validation of the hypothesis of eco-evolutionary dynamics within BEs has become a priority (e.g. Jones, 2012; Matthews *et al.*, 2014). The proposed models of biogeomorphic succession and biogeomorphic functional similarity at a global scale will help in testing the limits of the niche construction hypothesis because they offer a conceptual framework that helps to establish a causal relationship between selection of plant traits (response) according to the physical environment and the effects of plant traits on the physical environment.

Biogeomorphic ecosystem management and restoration

We also stress the opportunity presented by developing this worldwide model of biogeomorphic functional similarity for the restoration and management of BEs. The identification and quantification of key traits leading to establishment of viable populations of engineer species should become a priority for restoration in relation to their increase of ecosystem stability, specifically in the context of global change. The identification and 'use' of target response, effect and feedback traits associated with engineer plant species may represent a more efficient solution than the taxonomic approach for 'manipulating' BE resistance and resilience in the context of global environmental change. Comprehension and quantification of the natural dynamics of BEs to restore their dynamic biogeomorphic equilibrium according to the reciprocal dependency between engineer plant traits, independently from their biogeographic origin (i.e. native or exotic species) and a changing physical disturbance regime, offers great perspectives for orienting BEs gradually toward suitable target ecological states. The use of engineer species traits in such an ecological engineering context may promote sustainable restoration of services to society such as buffering against erosion and inundation (e.g. Byers *et al.*, 2006; Crain & Bertness, 2006; Temmerman *et al.*, 2013). In the context of global environmental change, the question of which

584 level (i.e. genes, population, community, landscape) should be manipulated will
585 certainly become crucial.

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796

797 **Biosketch**

798

799 The biogeomorphic research group which has collaborated for this article is
800 interested in studying feedbacks between plant dynamics and geomorphology within
801 various fluvial and coastal ecosystems around the world. All authors contributed
802 substantially in writing the article according to their experience of rivers (D. Corenblit,
803 E. González, V. Garófano-Gómez, A.M. Gurnell, B. Hortobágyi, F. Julien, L. Lambs,
804 J. Steiger, E. Tabacchi), salt marshes and mangroves (T. Balke, T. Bouma, D. Kim,
805 F. Fromard, R. Walcker) and coastal dunes (A. Baas, J.A. Stallins).

806

807 **Tables**

808 **Table 1.** Developmental sequence of biogeomorphic ecosystems (BEs) during the biogeomorphic succession and related plant
809 functional traits. The functional structure of a BE is shaped by a set of plant species specifically adapted to geomorphic
810 disturbances and to stress. Such species are related, for example within temperate fluvial BEs, to the genera *Alnus*, *Populus*, *Salix*,
811 and *Tamarix*; within tropical mangrove BEs to *Avicennia*, *Ceriops*, *Rizophora* and *Sonneratia*; within temperate salt marsh BEs to
812 *Juncus*, *Puccinellia*, and *Spartina*; and within temperate dune BEs to *Ammophila*, *Cakile*, *Panicum*, and *Uniolo*. Many species of
813 these genera developed similar functional response traits specifically related to regular and ordinary variations in hydrodynamic and
814 aerodynamic forces and also to a certain range of energy pulses and their subsequent consequences on sediment erosion,
815 transportation and deposition. Here, the common and specific functional traits of the four different BEs are listed and related to each
816 biogeomorphic succession phase.

Biogeomorphic succession phase	Duration of the BS phase	Main characteristics	Main geomorphic processes and landform formation	Main ecological processes	Common and specific plant functional traits
Geomorphic	Continuous at a local scale within certain locations (e.g. entrenched channels); enhanced by high frequency disturbances (e.g. convex bar formation during progressive meander migration in rivers) and tides within dynamic coastal zones Punctual at a larger scales; driven by low frequency floods and storms or tsunamis	Biogeomorphic rejuvenation and bare surface formation; BE structured mainly by geomorphic processes	Fluvial BEs: landform erosion and alluvial bar formation Salt marsh and mangrove BEs: landform erosion and tidal mudflat deposition Coastal dune BEs: beach/dune erosion and beach accretion	Diaspore dispersal; diaspore and organic matter deposition on open bare sediments	Common: short lifespan; production of numerous buoyant seeds and propagules; seed release synchronized with the flow regime Salt marsh and mangrove: vivipary and floating diaspores (longer lifespan in salty water)

Pioneer	Few days to few months	Establishment of bare surfaces. Geomorphic processes exert a strong and unidirectional control on organisms, filtering community composition	<p>Fluvial BEs: alluvial bar formation</p> <p>Salt marsh and mangrove BEs: tidal mudflat formation</p> <p>Coastal dune BEs: beach accretion</p>	<p>Recruitment</p> <p>Germination and sprouting on open bare sediments; seedling/resprout</p>	Common: rapid root anchoring; clonal growth from drifting debris and propagules; seedling tolerance to submersion and sediment burial
Biogeomorphic	Few years to few decades	Population establishment; engineer plants control geomorphology and respond to changes in geomorphic environment; overall strong feedbacks between biota and the physical environment	<p>Common: sediment accretion within and downstream/downwind vegetation patches</p> <p>Fluvial BEs: pioneer vegetated islands and benches</p> <p>Salt marsh BEs: tussocks, hummocks, vegetated tidal mudflat</p> <p>Mangrove BEs: vegetated tidal mudflat</p> <p>Coastal dune BEs: coppice dunes, hummocks, foredune, parabolic dune</p>	Dominance of engineer plants; facilitation for some other taxa; taxa exclusion; resource grab uptake in a more and more stabilizing habitat	<p>Common: high growth rate; rapid underwater shoot extension; tolerance to sediment burial and prolonged submersion; control of aboveground and belowground biomass allocation; changes in stem and root morphology and physiology in sediment deposit; shallow rooting; stem buoyancy</p> <p>Fluvial BEs: allocation to belowground biomass and branch sacrifice during the dry season; adaptation to hydrodynamics forces: high bending stability, flexible stems, narrow leaf shape, multi-stemmed resprouting from roots and shoots; brittle twig bases</p> <p>Salt marsh BEs: aerenchyma tissue for transferring oxygen from the atmosphere to submerged roots; tolerance to salt: succulence improving water retention, salt exclusion at the roots; salt excretion with glands.</p> <p>Mangrove BEs: adaptations to long submersion in salty water: aerenchyma tissue for transferring oxygen from the atmosphere to submerged roots; pneumatophores; salt excretion and</p>

					<p>exclusion; salt sequestration into leaves periodically shed; adaptation to hydrodynamics forces: spreading horizontal roots, prop and stilt roots, kneed roots</p> <p>Coastal dune BEs: anatomical adaptation to sediment abrasion</p>
Ecological	Few decades to few centuries	Older ecological succession (post-pioneer to mature stabilized stands); BE dominantly structured by biotic interactions	<p>Fluvial BEs: vegetated floodplains and mature islands</p> <p>Salt marsh BEs: raised vegetated tidal mudflat</p> <p>Mangrove BEs: raised vegetated tidal mudflat</p> <p>Coastal dune BEs: stabilized parabolic and plain vegetated dunes</p>	<p>Plant succession</p> <p>Increase of biotic interaction (e.g. competition and positive interactions) such as for example symbiosis)</p> <p>Pedogenesis</p>	Common: development of competitive traits (e.g. high size) to access resources more efficiently and reproduce in a stabilized environment

Figure legends

Figure 1. Global distribution of distinct fluvial and coastal biogeomorphic ecosystems (BEs). (a): River abundance by ecoregion defined from low (light blue) to high (dark blue) (Abell *et al.*, 2008), photo: J. Steiger; (b): salt marshes distribution (UNEP WCMC, 2013), photo: T. Balke; (c): mangroves distribution (Giri *et al.*, 2011), photo: T. Balke; (d): coastal dunes distribution (Martínez *et al.*, 2004), photo: J.A. Stallins.

Figure 2. Conceptual model of biogeomorphic succession (*sensu* Corenblit *et al.*, 2007, 2009a). Interactions between the physical (squares) and biological (circles) compartments are shown for each phase (inspired from Odling-Smee *et al.*, 2003). Arrows indicate an interaction with its intensity schematized by the size of line. The influence of engineering plants on the physical compartment is represented by a dark color within the squares. Physical changes related to early stages of the biogeomorphic phase correspond to sediment accretion and topographical raise; those associated with late stages of the biogeomorphic phase and to the ecological phase to changes in physicochemical properties of the soil.

Figure 3. Criteria related to the geomorphic setting and the nature of its relation with plant traits that a certain ecosystem has to satisfy in order to be identified as a biogeomorphic ecosystem (BE). Criterion 1: pioneer plants developed specific responses to the geomorphic environment (response traits); criterion 2: the geomorphic and physicochemical environment is modulated by engineer plants (effect traits); criterion 3: geomorphic changes under plant control feed back to organisms (feedback traits).

Figure 4. Exposure gradients to hydrogeomorphic and aerodynamic disturbances in fluvial and coastal biogeomorphic ecosystems (BEs). Hydrogeomorphic disturbance is represented in terms of water level variations for all the ecosystems and has different impacts depending on the specific biogeomorphic succession phase (represented in the line at the bottom of each ecosystem). The correspondence with the model of biogeomorphic succession (Fig. 2) is shown at the bottom of the figure.

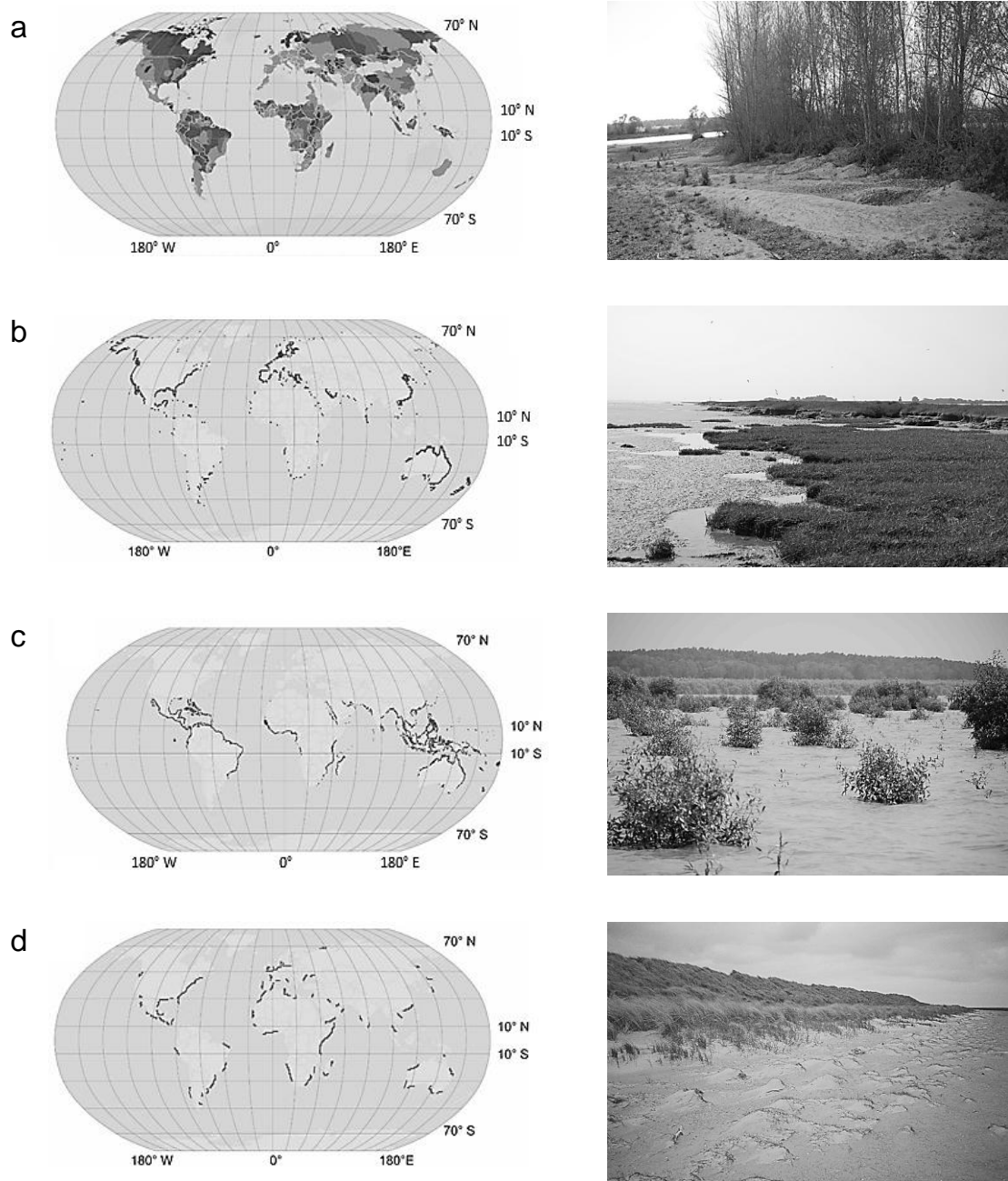
847 **Figures**

848 Figure 1.

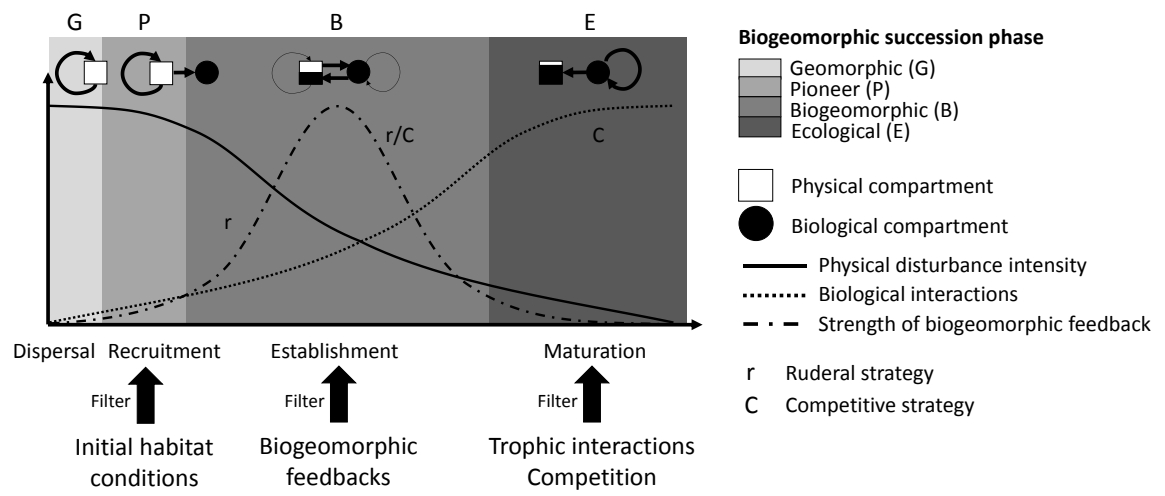
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850 Color fig.

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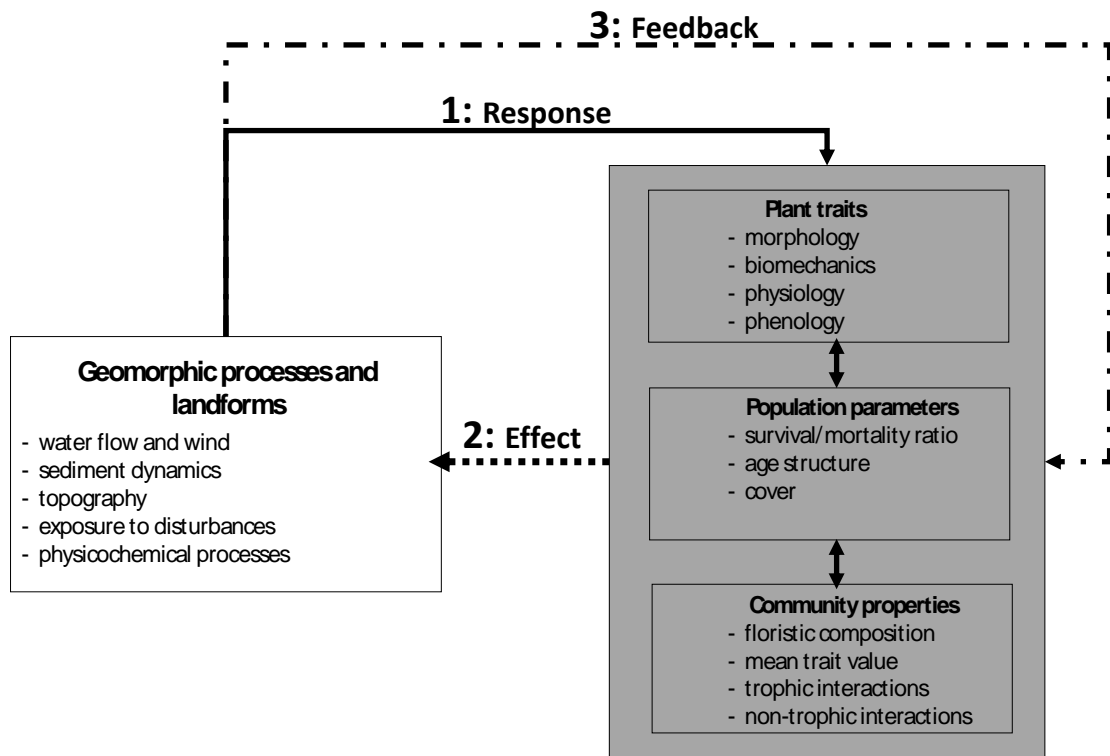


854 Figure 2.



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857 Figure 3.



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860 Figure 4.

861 Color fig.

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